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Landscape simplification weakens the association between terrestrial producer and consumer diversity in Europe

Running head: Diversity associations and land-use change

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Abstract

Land-use change is one of the primary drivers of species loss, yet little is known about its effect on other components of biodiversity that may be at risk. Here, we ask whether, and to what extent, landscape simplification, measured as the percentage of arable land in the landscape, disrupts the functional and phylogenetic association between primary producers and consumers. Across seven European regions, we inferred the potential associations

(functional and phylogenetic) between host plants and butterflies in 561 semi-natural grasslands. Local plant diversity showed a strong bottom-up effect on butterfly diversity in the most complex landscapes, but this effect disappeared in simple landscapes. The functional associations between plant and butterflies are, therefore, the results of processes that act not only locally but are also dependent on the surrounding landscape context. Similarly, landscape simplification reduced the phylogenetic congruence among host plants and butterflies indicating that closely related butterflies become more generalist in the resources used. These processes occurred without any detectable change in species richness of plants or butterflies along the gradient of arable land. The structural properties of ecosystems are experiencing substantial erosion, with potentially pervasive effects on ecosystem functions and future evolutionary trajectories. Loss of interacting species might trigger cascading extinction events and reduce the stability of trophic interactions, as well as influence the longer-term resilience of ecosystem functions. This underscores a growing realization that species richness is a crude and insensitive metric and that both functional and phylogenetic associations, measured across multiple trophic levels, are likely to provide additional and deeper insights into the resilience of ecosystems, and the functions they provide.

Introduction

Land-use simplification has emerged as one of the fundamental components of global change (Foley *et al.*, 2005; Turner II *et al.*, 2007; Verburg *et al.*, 2011; Allan *et al.*, 2015; Newbold *et al.*, 2015). Ecology has provided ample scientific evidence that decreasing habitat heterogeneity and increasing fragmentation, e.g. through agricultural expansion and intensification (a process often termed "landscape simplification") (Meehan *et al.*, 2011), are main anthropogenic drivers of biodiversity loss (Tscharntke *et al.*, 2012). However, biodiversity science has largely focused on species richness loss, underplaying other

components of biodiversity that may be at risk from landscape simplification (Valiente-Banuet *et al.*, 2015). Traditionally, studies have focused on a single trophic level, when instead the biodiversity loss at a given trophic level may also affect other levels, and, hence the associated diversity relationships (Duffy *et al.*, 2007; Scherber *et al.*, 2010). Associations between trophic levels can have a large impact on community responses to global change (Duffy, 2002; Cardinale *et al.*, 2012; Oliver *et al.*, 2015). Loss of interacting species can trigger cascading extinction events and reduce the stability of trophic interactions (Dunne *et al.*, 2002; Haddad *et al.*, 2011), as well as influence the longer-term resilience of ecosystem functions (Oliver *et al.*, 2015).

In many human-managed landscapes that are characterized by fragmented habitats, the resource base for consumers is often scattered across space (Tscharntke & Brandl, 2004; Winfree *et al.*, 2011). Because consumer insects are generally highly mobile and affected by land use change, landscape simplification can also alter the relationships between the diversity of different taxa (Tscharntke *et al.*, 2012; Weiner *et al.*, 2014). Our understanding of these associations is mainly based on analyses of manipulative experiments (e.g. Haddad *et al.*, 2009; Scherber *et al.*, 2010) or on observational studies at the local scale (e.g. Manning *et al.*, 2015), while empirical data considering the effect of land-use change at larger spatial scales are largely missing. For instance, it remains less clear how local associations between producer and consumer diversity are affected by landscape simplification. Nevertheless, focusing on the conservation status of local scale trophic associations can provide early diagnosis of the functional consequences of biodiversity loss due to global change (Valiente-Banuet *et al.*, 2015; Harvey *et al.*, 2016).

The potential functional associations between host plants and consumers (functional links; Fig. 1a) can be combined with phylogenetic information in order to indicate the degree of phylogenetic congruence (Ferrer-Paris *et al.*, 2013; Pellissier *et al.*, 2013). We expect that

consumers that are phylogenetically related feed on host plant species that are also phylogenetically related (phylogenetic links; Fig. 1b)(Ødegaard *et al.*, 2005; Weiblen *et al.*, 2006). Although congruent phylogenies are often considered as a signal of tight co-evolutionary associations between plants and insects, this pattern alone is not sufficient to demonstrate co-speciation (the matching of speciation events in two or more interacting taxa). There can be other non-coevolutionary processes that can produce congruent patterns (de Vienne *et al.*, 2013; Althoff *et al.*, 2014). For instance, some species-specific ecological traits and their geographical variation can generate such pattern. Host specificity, in particular, is expected to affect the extent of co-evolutionary associations (Clayton *et al.*, 2004).

Here, we ask whether, and to what extent, landscape simplification, measured as the percentage of arable land in the landscape, has disrupted functional and phylogenetic associations between plants and butterflies. This landscape metric has been used as a relevant proxy for characterizing landscape simplification (Tscharntke *et al.*, 2005) and agricultural intensification (Meehan *et al.*, 2011). Depending on the degree of specialization, butterflies are functionally linked to one or more host plant species, both as herbivores at the larval stage and as flower-visitors as adults (Fig. 1a). First, we hypothesize that variation in host plant diversity would mediate the abundance distribution and species richness of butterfly communities (Fig. 1a) and that landscape simplification can disrupt these relationships (Fig. 1 c). The loss of functional associations might occur in the absence of local species loss. For instance, a substantial decline in abundance can lead to the loss of interactions with other species without causing local extinction (Estes *et al.*, 1989; McConkey & O'Farrill, 2015). This loss of functional relationships is likely to be more evident in human-altered ecosystems (Chapin III *et al.*, 2000). Second, we determined whether landscape simplification undermined the degree of phylogenetic congruence in the potential host plant-butterfly

linkages. We estimated the degree of phylogenetic congruence for each site and tested the probability of observing significant signals in relation to landscape simplification. Then, using a randomization approach, we investigate whether the observed signal was likely to be due to specialization rather than deeper co-evolutionary history (Clayton *et al.*, 2004; Althoff *et al.*, 2014). We predicted that the loss of specialist species due to landscape simplification (Öckinger *et al.*, 2010; Weiner *et al.*, 2014) weakens the signal of phylogenetic congruence.

Materials and methods

Studies

We used primary data from seven independent regions across four European countries (Finland, Italy, Sweden, and UK) where data on butterfly and plant composition were available for the same sites (Marini *et al.*, 2009, 2014; Pöyry *et al.*, 2009; Gabriel *et al.*, 2010; Hambäck *et al.*, 2010; Öckinger *et al.*, 2010, 2012; Dainese *et al.*, 2015) (Appendix S1, Table S1 in Supporting Information). Observations were conducted in different types of semi-natural grasslands, such as field margins, meadows, and pastures. All data sets were collected over one season, except for the UK study where two sampling years were available. Overall, 561 sites in eight datasets were included (area ranged from from 50 m^2 to 26.6 ha). Vascular plants and butterflies were sampled by plot counts or transect walks with the transect length and search time proportional to habitat area. A summary of the data sources and sampling methods is provided in Appendix S1 (Table S1). The percentage of arable land surrounding each study site was used as a measure of landscape simplification (**LS**) and was calculated at three spatial scales (0.5, 1, and 2 km). For the studies where this information was not available, we calculated the percentage of arable land using a detailed vector-based land-cover map (specific for each region). The range of arable cover in the landscape was usually large, and there

was a good overlap between the different regions (Appendix S1, Table S1).

Matrix calculation

Data on species composition deriving from each dataset were merged into two matrices: a butterfly species-by-site matrix (**B**) and a plant species-by-site matrix (**P**) (Appendix S1, Fig. S1). For each country, we compiled a list of butterfly-host plant associations derived from scientific literature and validated by experts (Appendix S1, Table S2). In this way, we accounted for the potential geographical variation in host plant use. Only the butterfly species that feed on herbaceous species were used in the butterfly-host plant association. When a butterfly species feeds on multiple host species of an entire family (e.g., *Coenonympha pamphilus* feeding on numerous *Poaceae* spp. or *Colias crocea* feeding on numerous *Fabaceae* spp.), we used the family taxonomic level in the list. The same approach was adopted for a butterfly species feeding on several species of a genus (e.g., *Argynnis aglaja* or *Boloria selene* feeding on *Viola* spp.), i.e. in these cases we used the genus taxonomic level in the list. In these cases, we assume that the occurrence of a butterfly depended on the presence of host family or genus in the plant community and not by the number of species belonging to that family or genus. As a result, the host plant list included different taxonomical levels, such as species, genus, or family. Since many butterfly species are polyphagous (species feeding on plants belonging to different families), we could have multiple hosts associated with a single butterfly. We converted the association list into an interaction matrix (**HB**) between host plants (rows) and butterfly species (columns) occurring in the datasets and based on a binary association index (0 = absence and 1 = presence) (Appendix S1, Fig. S1). From the plant species-by-site matrix (**P**), we built two sub-matrices: a host plant-by-site matrix (**H**) and a flowering forb species-by-site matrix (**F**) (Appendix S1, Fig. S1).

The host plant species-by-site matrix (**H**) was built using the host plant list derived from the association matrix **HB**. When a family or genus characterized the host plant, the weight of all species belonging to the same family or genus and occurring in the community was equal to one (e.g., if a generalist butterfly fed on numerous *Poaceae* spp. and there were five plant species in this family in the community, we scored each species as 0.2 when we calculated host plant richness). Similarly, when multiple butterflies were associated with a single host plant, this host plant had a weight equal to one in the community. In this way, we avoided bias created by overweighing the number of host plants belonging to the same family/genus or associated to various butterflies. As butterflies show low specialization during adult feeding (Rosas-Guerrero *et al.*, 2014), we considered all the nectar plants occurring in the communities to build the flowering forb species-by-site matrix (**F**) (Appendix S1, Fig. S1).

Traits and phylogeny

For flowering forb species, we selected traits that captured key aspects of floral display and phenology and for which data were available. The selected traits were as follows: (i) flower size, (ii) flower color, (iii) flower morphology, and (iv) flowering period. As a result, a species-by-trait matrix was built (**T**) (Appendix S1, Fig. S1). For flower size, we considered the flower diameter in mm. In the absence of more adequate color classification (e.g. spectral reflectance data), we classified flower color in classes as seen by humans, since previous studies found a significant relationship to visitation patterns of pollinators (Eklöf *et al.*, 2013; Carvalheiro *et al.*, 2014). We classified the plant species in four classes of flower color: white, yellow, warm colors (pink – red – purple), and cold colors (violet – blue). For flower morphology, we classified the plant species into five main categories according to blossom type (Pellissier *et al.*, 2010): disk (plane- or bowl-

shaped actinomorphic blossoms with easily attainable pollen and nectar), funnel (open stereo- and actinomorphic blossoms with a wide opening and a typical 'bell-shape' with easily attainable pollen and nectar), bilabiate (zygomorphic blossoms in which pollen is placed dorsally or ventrally on the pollinator), tube (actinomorphic blossoms forming a long tube with nectar hidden at the bottom), and head (flat or globular blossoms composed of tightly arranged small actinomorphic or zygomorphic flowers). Flowering period was defined as the number of months over which a plant species usually blossoms. Trait data were derived from different sources (Klotz *et al.*, 2002; Aeschimann *et al.*, 2004; Royal Botanic Gardens Kew, 2014).

For butterflies, host plant specialization (larval feeding niche diet breadth) was measured using the number of larval host plants species derived from the butterfly-host plant association list. Species whose larval feeding niche consisted of a single plant genus were classified as food specialists whereas species feeding on more than one genus were classified as generalists (Öckinger *et al.*, 2010). For each site, we calculated the proportion of specialist species out of the total species richness.

For the host plants ($\mathbf{H_P}$) (Appendix S1, Fig. S1 and Appendix S2), we calculated a phylogenetic tree using Phylomatic version 3 (http://phylodiversity.net/phylomatic/) and derived from the Phylomatic megatree (R20120829) based on the APG III classification (Bremer *et al.*, 2009). For butterflies, we built an updated molecular phylogeny for 115 species (**B**), using cytochrome oxidase subunit I (COI) gene sequences that were extracted from GenBank (Benson *et al.*, 2011) (Appendix S2). Both phylogenetic trees were built considering the whole dataset.

Butterfly and plant community components

For each site, three community components were calculated for butterflies (calculated using matrix **B**): total abundance (**B_{AB}**), evenness (**B_{EV}**), and species richness (**B_{SR}**) (Appendix S1, Fig. S1). Evenness (**B_{EV}**) was calculated using the E_{var} index (Smith & Wilson, 1996):

$$E_{var} = 1 - \frac{2}{\pi} arctan\left\{\frac{1}{S}\sum (ln(p_i) - \mu_{ln})^2\right\}$$

where $\mu_{ln} = \frac{1}{S}\sum \ln(p_i)$ and p_i is the relative abundance of species. The formula is based on the variance of log abundances (centered on the mean of log abundances) then appropriately scaled to cover 0-1 (0 = maximally uneven and 1 = perfectly even). This index is mathematically independent from species richness (Appendix S1, Fig. S2 and S3).

For plants, we considered five community components: species richness, evenness, functional diversity, functional trait composition, and phylogenetic diversity. Species richness and evenness were estimated for both host plants (matrix $\mathbf{H} \rightarrow \mathbf{H_{SP}}$ and $\mathbf{H_{EV}}$) and flowering forbs (matrix $\mathbf{F} \rightarrow \mathbf{F_{SP}}$ and $\mathbf{F_{EV}}$), functional diversity and functional trait composition only for flowering plants (matrix $\mathbf{F} \rightarrow \mathbf{F_{FD}}$ and $\mathbf{F_{FC}}$), and phylogenetic diversity only for host plants (matrix $\mathbf{H} \rightarrow \mathbf{H_{PD}}$) (Appendix S1, Fig. S1). Evenness was calculated using the E_{var} index as for butterflies. Functional diversity (**F_{FD}**), based on multiple traits in matrix **T**, was measured using the standardized effect size (SES) of the abundance-weighted mean pairwise distance (MPD) among species in a site (Swenson, 2014), as implemented in the 'picante' R package. The MPD index is equivalent to Rao Quadratic Entropy Index of Diversity (Rao, 1982), as demonstrated in simulated (Mouchet *et al.*, 2010) and empirical data (Ricotta & Moretti, 2011). The trait matrix was converted into a Gower distance matrix, which allows mixing different types of

variables. This in turn was converted into a functional dendrogram by a UPGM clustering analysis and used to calculate the MPD (Swenson, 2014). Flower size (continuous trait) was log-transformed before calculation. Since the variance of MPD strongly depends on local species richness (Swenson, 2014), the observed values of MPD were standardized. To calculate the SES, MPD was centered and scaled using the mean and standard deviation estimates based on the distribution of the corresponding indices calculated for 999 null communities as follows:

$$SES = \frac{MPD_{obs} - mean(MPD_{null})}{\sigma(MPD_{null})}$$

The null communities were generated with species richness equal to each of the observed assemblages and species selected at random from the regional species pool of the observed community. The functional trait composition of the local plant community ($\mathbf{F_{FC}}$) was estimated using the community-weighted mean (CWM) for each plant trait separately ($\mathbf{F} \times \mathbf{T} \rightarrow \mathbf{F_{FC}}$) (Appendix S1, Fig. S1). CWM represents the average trait value in a community weighted by the relative abundance of the species carrying each value (Garnier *et al.*, 2004):

$$CWM = \sum_{i=1}^{S} p_i x_i$$

where x_i is the mean trait value of the i-th species (the average over all trait measures for a given species; for binary traits x_i can be either 0 or 1 and the index reflects the relative abundance of each category), and p_i is the proportion of that species. A principal component analysis (PCA) was then used to reduce trait redundancy and to produce orthogonal axes of functional trait composition (Appendix S1, Fig. S4). We ran the PCA on the CWM trait matrix ($\mathbf{F_{FC}}$), standardized to mean 0 and unit variance. The PCA site-

score data in two-dimensional trait-space ($\mathbf{F_{FC1}}$ and $\mathbf{F_{FC2}}$) was then used in the statistical modeling (Appendix S1, Fig. S1). The first two axes of PCA explained about 37% of total variation. The first principal component ($\mathbf{F_{FC1}}$) that accounted for 22% of the functional trait composition variation had high positive loadings for flower size, warm colour flowers, and head blossoms, as well as high negative loadings for white colour flowers and disk blossoms (Appendix S1, Fig. S4). The second principal component ($\mathbf{F_{FC2}}$) explained 15% of functional trait composition variation. This axis had high positive loadings for yellow colour flowers and negative loadings for cold colour flowers (Appendix S1, Fig. S4). Phylogenetic diversity ($\mathbf{H_{PD}}$) was calculated using the standardized effect size (SES) of the mean pairwise phylogenetic distance (MPD) among species in a site. In this case, the null communities were generated by randomly reshuffling the tip labels on the host plant phylogeny, while preserving community composition and related patterns (species richness, species frequency and co-occurrence patterns across communities).

Phylogenetic congruence of butterfly-host plant associations

For each site, phylogenetic trees were pruned from the reference host plant ($\mathbf{H_P} \rightarrow \mathbf{H_{P}}_i$) and butterfly ($\mathbf{B_P} \rightarrow \mathbf{B_{P}}_i$) phylogenies to include only species (family, genus and/or species for host plants) occurring in the site. The same procedure was repeated for the association matrix ($\mathbf{HB} \rightarrow \mathbf{HB}_i$). At each site, we tested the congruence between butterfly and host plant phylogenies using the ParaFit test, implemented in the 'ape' R package, a method originally developed for the co-evolutionary analyses of hosts and parasites (Legendre *et al.*, 2002). ParaFit is a matrix permutation test of co-speciation, which aims to test whether interactions between trophic levels are phylogenetically

correlated. The null hypothesis is that butterflies utilize resources randomly with respect to the phylogenetic tree of the host plants while the alternative hypothesis is that butterflies and their host plants occupy corresponding positions in their phylogenetic trees. This method is advantageous because it can accommodate cases where multiple butterflies are associated with a single host plant, or when multiple hosts are associated with single butterfly species, and it can be used to assess the contribution of each individual butterfly–host plant link to the total congruence statistics (de Vienne *et al.*, 2013). Distance matrices for butterflies ($\mathbf{B_{P}}_{i} \rightarrow \mathbf{dB_{P}}_{i}$) and host plants ($\mathbf{H_{P}}_{i} \rightarrow \mathbf{dH_{P}}_{i}$) were derived from the phylogenies using the 'cophenetic' function in the 'ape' R package. The test was performed for each site (local scale) separately and included a phylogeny for both the trophic levels ($\mathbf{dB_{P}}_{i}$ and $\mathbf{dH_{P}}_{i}$) and a consumer (butterfly) × resource (host plant) species interaction matrix ($\mathbf{HB}_{i}$) (Fig. S1). A global statistic was then derived from each site (Parafit test with 999 permutations). We also performed the test for each data set (regional scale) separately (Appendix S1, Fig. S5). We converted the *P* value derived from Parafit test into a binary index, where sites with significant phylogenetic congruence were coded as 1 and non-significant as 0.

To test whether the ParaFit results were not simply a result of specialization but also of tight co-evolution (Clayton *et al.*, 2004), we repeated the ParaFit test maintaining the same consumer (butterfly) × resource (host plant) species interaction matrix ($\mathbf{HB}_{i}$) but randomizing the tips on the butterfly phylogeny (see Jenkins *et al.*, 2012). In this way, we preserved the same number of associations per butterfly, while randomizing the evolutionary history among them. If the phylogenetic congruence of butterfly-host plant associations remains intact even after this randomization approach, butterfly specialization can be considered the process that produces the congruent patterns.

Finally, we conducted an additional analysis to test whether the ParaFit results

were affected by the fact that some butterflies were linked to many host plants, while others to only one. When a butterfly species feeds on multiple species of an entire family, we used only one link between a butterfly and a random member of a plant family.

Statistical analysis

All analyses were conducted using R version 3.0.4 (R Foundation for Statistical Computing, Vienna, Austria, 2014). Before performing the analyses, diversity measures were standardized using z-scores $\left(\frac{y_i-\bar{y}}{SD_y}\right)$ within each study to allow comparisons between studies with contrasting means $\bar{y}$ and standard deviations SD_y, and differences in methodology. We tested the influence of plant diversity measures on butterfly abundance, evenness, and richness using linear mixed-effects models (LMMs) with Gaussian error distribution. To account for differences in methods between the studies, we included study identity as a random factor (i.e., the model estimated different intercepts α_i for each study i). Model residuals were approximately normally distributed and exhibited homogeneity of variance. All the LMMs were estimated using the 'lme4' package in R. We built three models that tested the interactive effect of plant diversity measures and landscape simplification on butterfly (*i*) abundance, (*ii*) evenness, and (*iii*) richness. We assume that butterfly abundance was affected by flower functional traits (i.e. community characteristics that affect adult butterflies), whereas butterfly evenness and species richness were affected by host plant diversity (i.e. community characteristics that reflect butterfly larvae feeding) (Fig. 1). In a fourth model (*iv*), we related the phylogenetic congruence signal to landscape simplification.

(i) Influence of local habitat quality and landscape simplification on butterfly abundance

(hypothesis i). Due to a low specialization between adult butterflies and flower resources, we hypothesize that local habitat quality (i.e. diversity of flower resources) is strongly correlated with butterfly abundance. In this model, we tested the interactive effects of landscape simplification and local habitat quality, measured by flowering forb species richness, functional diversity, and functional trait composition (the two orthogonal axes derived from the PCA on the CWM trait matrix) on butterfly abundance.

As butterflies are more specialized to host plants at the larval stage, we hypothesize in models *ii* and *iii* that variation in host plant diversity has instead the main influence on the evenness and species richness of butterfly communities. We assessed the robustness of hypotheses *ii* and *iii* by including flowering forb evenness or richness in the models.

(ii) Influence of host plant evenness and landscape simplification on butterfly evenness (hypothesis ii). We tested the interactive effect of landscape simplification and local host plant evenness on butterfly evenness. Flowering forb evenness was also included in the model.

(iii) Influence of host plant diversity and landscape simplification on butterfly richness (hypothesis iii). We verified the interactive effects of landscape simplification and host plant diversity (richness and phylogenetic diversity) on butterfly species richness. It was not possible to include both measures of host plant diversity in the same model, due to problems of convergence. Similarly, flowering forb diversity was collinear with host plant richness. Therefore, we estimated the effects of these variables by fitting three separate models and using the Akaike information criterion (AIC) to determine the best model.

(iv) Influence of landscape simplification on phylogenetic congruence among host plants and butterflies (hypothesis iv). We verified whether landscape simplification negatively affected the congruence between butterfly and host plant phylogenies, measured as the proportion of sites with significant phylogenetic congruence. The proportion of sites with significant congruence was analyzed using a generalized linear mixed-effects model with binomial error distribution. Then, we tested the relationship between butterfly specialization (i.e. the proportion of specialist species) and the proportion of sites with significant congruence. Finally, to verify whether the changes in butterfly specialization drove the shifts in phylogenetic association with landscape simplification or a tight co-evolution signal was also involved, we repeated the analysis considering the proportion of sites with significant congruence derived from the ParaFit analysis with the randomized butterfly tips. The significance of landscape simplification was determined with parametric bootstrapping with 1000 bootstrap replicates.

Model selection. As two sampling years were available for the UK study, we compared the models considering both years and only one year at a time. The results were qualitatively equal between the models. In all the models we present results considering both years for the UK study. For each model (*i-iv*), we tested the effect of landscape simplification (i.e. the percentage of arable land in the landscape) using the three landscape scales (0.5, 1, 2 km) separately. We selected the radius that had the strongest effect on model results, that is, with the lowest AIC value (Appendix S1, Table S3). Models including landscape simplification measured with a radius of 2 km had the lowest AIC in almost all the cases, even though the magnitude of the differences were quite similar among the landscape scales (Appendix S1, Table S3). The radius of 2 km has been previously found to be an appropriate scale for modeling butterfly species

diversity (Krauss *et al.*, 2010; Bommarco *et al.*, 2014). Therefore, we present the results using the same scale with a 2 km landscape buffer for all the models. In the models relating to hypotheses *i-iii*, we applied an information-theoretic model selection procedure to evaluate alternative competing models (Burnham & Anderson, 2002). We compared the fit of all possible candidate models obtained by the combination of the predictors using second-order Akaike's information criterion (AICc). Then, we ranked the models according to their AICc, identified top models (i.e. ΔAICc from the best model < 7) for each hypothesis, and calculated associated Akaike weights (w_i) for each parameter, we used model averaging based on the 95% confidence set to incorporate model selection uncertainty into our parameter estimates (Burnham & Anderson, 2002). We also report 95% confidence intervals (CIs) around model-averaged partial slope coefficients. Akaike weights (w_i) were used to measure the relative importance of each covariate, summing w_i across the models ($\sum w_i$) in which the covariate occurred. Covariates were considered important if they appeared in top models (ΔAICc < 7) and had a sum of model weights > 0.6. Unconditional CIs that did not include 0 indicated a significant effect. Model comparison was implemented using the 'MuMIn' package in R.

Results

Effect of landscape simplification on functional associations

We found a positive effect of flowering plant species richness ($\sum w_i = 1.00$; $\beta = 0.242$) and plant functional trait composition ($\sum w_i = 0.99$; $\beta = 0.067$) on butterfly abundance (Appendix S1, Table S4). Specifically, butterfly abundance was highest on sites with many large warm-coloured flowers, head blossoms and flowers aggregated into flower heads. Second, host plant communities with high evenness supported butterfly communities with high evenness ($\sum w_i = 0.83$; $\beta = 0.067$) (Appendix S1, Table S4). Third, we detected a positive effect of both

host plant richness ($\sum w_i = 1.00$; $\beta = 0.278$) and flowering plant species richness ($\sum w_i = 1.00$; $\beta = 0.326$), but not of host plant phylogenetic diversity ($\sum w_i = 0.35$; $\beta = 0.012$), on butterfly species richness (Appendix S1, Table S4). Models performed using Chao 1abundance-based species richness estimator for butterflies confirmed the same results ($\sum w_i = 1.00$; $\beta = 0.212$ and 0.219 with host plant richness or flowering species richness, respectively) (Appendix S1, Table S4).

Analyzing the effects of the surrounding landscape on local communities of plants and butterflies, we found that all the potential functional associations described above were disrupted by landscape simplification (Fig. 2). The effect of local plant functional trait composition on butterfly abundance was positive only in the least simplified landscapes, but this effect disappeared in simple landscapes (Fig. 2b). A similar pattern was observed for the relationship between host plant and butterfly evenness (Fig. 2c). In the case of butterfly species richness, the positive effect of host plant richness disappeared at high levels of landscape simplification and was weak at intermediate levels (Fig. 2d).

Models containing host plant diversity showed a higher AIC (AIC = 1537.8 for host plant richness and AIC = 1585.7 for host plant phylogenetic diversity) than those containing flowering plant richness (AIC = 1521.1). However, the model with host plant richness was the most robust in maintaing the significant interaction between host plant richness and butterfly species richness with landscape simplification when we repeated the analysis using the Chao 1 abundance-based species richness estimator for butterflies. Instead, for flowering plant species richness this interaction was no longer significant ($\sum w_i = 0.25$; $\beta = -0.002$) (Appendix S1, Table S4). There was also no interactive effect in the model including host plant phylogenetic diversity as a predictor ($\sum w_i = 0.09$; $\beta = -0.003$).

Despite the strong effect of landscape simplification on functional associations, we found no impact of cover of arable land in the landscape on butterfly species richness (β = -0.002 P = 0.170, Fig. 3a), abundance (β = -0.0005, P = 0.746, Fig. 3a) and evenness (β = -0.0004, P = 0.815, Fig. 3a) or plant species richness (flowering plants: β = –0.001, P = 0.383, Fig. 3b; host plants: β = –0.002, P = 0.258, Fig. 3c).

Effect of landscape simplification on phylogenetic congruence

We found a significant phylogenetic congruence among host plants and butterflies for all the data sets (P < 0.001; Appendix S1, Fig. S5). At the local scale, a phylogenetic congruence was found in 51.0% of the sites (286 out of 561 sites, median P = 0.010). Reducing the number of associations to one host plant per butterfly gave similar results (42.2% of the sites had a significant associations, median P = 0.012). Testing for butterfly specialization by randomizing the butterfly tips, although maintaining the same host trees and association matrix showed weaker evidence of phylogenetic congruence (24.2% of the sites had a significant associations, median P = 0.200).

Landscape simplification reduced the phylogenetic congruence, as indicated by a negative relationship between the probability of observing a phylogenetic congruence and the cover of arable land (β = −0.014; CIs = –0.029, −0.003; P = 0.019) (Fig. 4a). The same pattern was confirmed using the reduced number of associations to one host plant per butterfly (β = −0.019; CIs = −0.035, −0.003; P = 0.018). Phylogenetic congruence was positively related to the proportion of butterfly specialists (β = 0.024; CIs = 0.008, 0.037; P = 0.001) (Appendix S1, Fig. S6). However, the negative relationship between landscape simplification and phylogenetic congruence was not confirmed considering the randomized butterfly tips (i.e. no effect of landscape simplification on phylogenetic congruence; β = –0.008, CIs = –0.023, 0.008; P = 0.316) (Fig. 4b).

Discussion

Our results provide clear evidence that landscape simplification weakens the functional and phylogenetic association between terrestrial producer and consumer diversity. In accordance with our hypotheses, the observed loss of functional and phylogenetic associations with increased landscape simplification occurred even without immediate reductions in species richness. Although this effect is not completely surprising, given the strong interaction between plant community characteristics and landscape simplification, it could be detrimental for specialized species in the long term (Tilman *et al.*, 1994; Kuussaari *et al.*, 2009), as local extinction of species could occur with a substantial delay following landscape simplification (Kuussaari et al., 2009). The consumer-mediated losses in host plant species could be less pronounced than those of resource-mediated losses in consumers, but these effects could be reversed in the long term as plant reproductive fitness and outcrossing may become at risk (Weiner *et al.*, 2014).

Local plant diversity showed a strong bottom-up effect on butterfly diversity in the most complex landscapes, but this effect disappeared in simple landscapes. The functional associations between plant and butterflies are, therefore, the results of processes that act not only locally but are also dependent on the surrounding landscape context (Tscharntke *et al.*, 2012). Landscape simplification can alter such associations through habitat loss and fragmentation. Probably, the greater habitat diversity and the higher proportion of semi-natural habitats in complex landscapes positively affect the local persistence of specialist butterfly species (Öckinger *et al.*, 2010). Generalist species are less susceptible to fragmentation because they are likely capable of finding alternative resources in simplified landscapes (Öckinger *et al.*, 2010). Hence, the higher degree of butterfly host plant specialization in complex landscapes would explain the strong relationship between host plant diversity and butterfly diversity (Weiner *et al.*, 2014). Consequently, this could benefit

the stability of trophic interactions through resource diversity, in part by reducing the runaway consumption of plants (Haddad *et al.*, 2011; Carvalheiro *et al.*, 2014).

Another important finding of this study is the importance of plant diversity in determining the structure of consumer communities in complex landscapes (Scherber *et al.*, 2010). Consequently, positive bottom-up effects of plant diversity on higher trophic levels could benefit trophic stability by reducing the variability in herbivore abundance and diversity within sites (Haddad *et al.*, 2011; Borer *et al.*, 2012). Although it has been argued that adult butterflies are often generalist feeders with low specialization on specific plant traits (Hardy *et al.*, 2007), our results reflect potential non-random interactions between flowers and adult butterflies. This would indicate a certain degree of floral specialization among butterfly species to a set of floral traits such as flower size, color, morphology, and nectar content (Junker *et al.*, 2013; Carvalheiro *et al.*, 2014; Curtis *et al.*, 2015; Lebeau *et al.*, 2016). Our findings also highlight the limitation of using plant phylogenetic diversity to predict butterfly diversity. Similar results have been found in other studies (Whitfeld *et al.*, 2012; Pellissier *et al.*, 2013), suggesting that a global measure of diversity of plant lineages does not necessarily reflect the associations between hosts and consumers. Plant phylogenetic diversity seem to be a better predictor of butterfly phylogenetic diversity given the co-evolution signal found in complex landscapes.

Our results revealed that landscape simplification also reduced the phylogenetic congruence among host plants and butterflies. The weaker congruence among host plant and butterfly phylogenies in highly modified landscapes indicates that closely related butterfly species are more generalist in the potential resource lineages used (Pellissier *et al.*, 2013). Although specialization is a necessary precondition for phylogenetic congruence, this is not necessarily indicative of co-speciation because species can descend from a generalist ancestor (Clayton *et al.*, 2004; de Vienne *et al.*, 2013; Althoff *et al.*, 2014). However, the change in

butterfly specialization is not the only process underpinning shifts in phylogenetic association with landscape simplification, suggesting a potential effect on co-evolutionary relationships between host plants and butterflies (Jenkins *et al.*, 2012). Indeed, a tight signal of co-evolution was found by randomizing the tips of butterfly trees in the phylogenetic congruence analysis (i.e. this resulted in a nonsignificant fit between host plant and butterfly associations). A signal of co-evolution was evident in complex landscapes, while was lost with landscape simplification. This could be because butterfly species do not feed anymore on closely related host plants due to a breakdown of co-evolutionary associations with landscape simplification. These processes could have pervasive effects on ecosystem functioning. Altering plant-consumer interactions could impact the fitness of both partners affecting population growth and, in the long term, the co-evolutionary relationships among species (Agrawal *et al.*, 2006). For instance, given the role of insect herbivores in the diversification of plant species and their traits, the loss of plant-consumer associations has potential to alter ecological and evolutionary dynamics in plant populations and communities (Agrawal *et al.*, 2012). Consequently, herbivore populations could evolve adaptations to these changes in the plant community, such as host shifts (Singer *et al.*, 1993). However, this could increase the risk of extinction, because ongoing land use changes are happening more rapidly than the adaptation that the insects can evidently realize (Singer *et al.*, 1993; Koh *et al.*, 2004; Krauss *et al.*, 2010; Scheper *et al.*, 2014). Koh *et al*. (2004) have demonstrated that a large number of butterfly species are already "co-endangered" as their host species are currently listed as endangered, indicating a need to increase current estimates of extinction risk by taking species co-extinctions into account. These co-extinctions can lead to the loss of irreplaceable evolutionary and co-evolutionary history (Purvis *et al.*, 2000) that has contributed to creating a high diversity of plant and butterfly species (Fordyce, 2010). While land-use change remains the predominant threat to species persistence and thus to trophic

associations, climate change could also dramatically alter these associations by shifting the geographic distribution of species and driving spatial or temporal mismatches among previously co-occurring species (Thackeray et al., 2010; Colwell et al., 2012).

From an applied perspective, there is a lack of specific reference to species interactions among conservation initiatives, probably because the importance of such interactions is not well understood yet (Soulé *et al.*, 2005). Conservation efforts might fail if we do not consider how landscape simplification affects the cross-trophic-level diversity associations in a local community (Harvey *et al.*, 2016). For instance, conservation interventions aimed at restoring consumer diversity by enhancing local plant resources is likely to be more effective in regions where landscape simplification has been less marked. Therefore, we suggest that monitoring of the relationships between the diversities of these taxa can serve as an early warning signal of ecosystem health and conservation status (Valiente-Banuet *et al.*, 2015). In conclusion, although most of the research on biodiversity loss have largely focused on species richness of individual taxonomic or functional groups, our novel approach reveals that other components of biodiversity are lost well before the species richness variation. Our measures of functional and phylogenetic associations across trophic levels, and how they change in response to landscape simplification, can contribute to a growing understanding of the properties that determine ecosystem resilience.

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Figure Captions

Figure 1. Schematic representation of potential associations between plants and butterflies and the expected landscape effect on these associations. (a) Butterflies have distinctive functional links with plants: they feed on plant tissues as larvae and on nectar as adults. As adult butterflies show low specialization with flower resources (Rosas-Guerrero et al., 2014) and we hypothesize that butterfly abundance depends on the species richness of flowering plants and their functional trait composition. The diet breadth of butterfly larvae is more restricted than that of adults due to (b) co-evolution between host and consumer (phylogenetically closely related butterflies often prefer to feed on phylogenetically closely related host plants). Such functional and phylogenetic associations determine the bottom-up effect of host plant diversity on butterfly evenness and species richness. (c) As losses of producer-consumer diversity associations may frequently precede the loss of species, we hypothesize a stronger negative effect of landscape simplification on producer-consumer diversity associations than on species richness loss.

Figure 2. The interactive effect of plant diversity and landscape simplification on butterfly diversity. (a) Panels are ranked from left to right according to increasing proportion of arable land cover in a radius of 2 km surrounding each site. (b) The interaction between plant functional trait composition and landscape simplification on butterfly abundance ($\sum wi = 0.93$; ß = −0.0033). Functional trait composition is a measure of the extent to which plant communities contain large flowers with warm

colors and head blossoms (Fig. S4). (c) The interaction between host plant evenness and landscape simplification on butterfly evenness (∑wi = 0.63; ß = −0.0043). (d) The interaction between host plant richness and landscape simplification on butterfly species richness (∑wi = 0.75; ß = −0.0041). The fitted lines (b-d) are general linear mixed model estimates calculated from the best plausible model (Table S4). The points represent the 561 study sites and show the partial residuals. Diversity measures from each study were standardized to z-scores prior the analysis.

Figure 3. (a) Relationship between butterfly species richness and landscape simplification. (b) The relationship between flowering plant species richness and landscape simplification. (c) The relationship between host plant richness and landscape simplification. The fitted lines (a-c) are general linear mixed model estimates.

Figure 4. Relationship between phylogenetic congruence signal and landscape simplification. (a) The proportion of sites with significant phylogenetic congruence signal derived after testing for global congruence in the local trophic networks. (b) Analysis conducted considering randomized butterfly tips. Landscape simplification was measured as the proportion of arable land cover in a radius of 2 km surrounding each site. Fitted line is a generalized linear mixed model estimate.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary Tables (S1-S4) and Figures (S1-S6).

Appendix S2. Phylogeny.